Do the dominant plant species impact the substrate and vegetation composition of post-coal mining spoil heaps?

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Abstract

Dominant species influence both species and functional composition of the vegetation as well as soil properties of the substrate. However, knowledge about the role played by dominant species in the process of shaping their habitat within post-industrial ecosystems is still limited. We aimed to assess the impact of four dominant species (Calamagrostis epigejos, Daucus carota, Poa compressa and Tussilago farfara) on soil abiotic and biotic properties, and to detect differences in species and functional composition of the vegetation types studied. We hypothesized that (1) dominant species of higher mean biomass cause lower aboveground biodiversity and (2) dominant species of higher mean biomass have a higher impact than the others on soil properties. We measured soil chemistry (TOC, N, P, K, Na, Mg content, EC, pH and enzyme activities) as well as biomass, species diversity and functional diversity of vegetation on 15 study plots (28.3 m2) for each species studied.

The DCA analysis revealed a clear distinction between the patches dominated by studied species. Vegetation patches dominated by Calamagrostis epigejos were correlated with amount of biomass, canopy height CWM and specific leaf CWM. Patches dominated by Daucus carota were related to the light requirements (EIV-L), Total Organic Carbon (TOC) and K content. The vegetation patches dominated by Poa compressa were related to dehydrogenase activity, higher Mg content and species richness of the vegetation patches. The highest TOC content was recorded for T. farfara substrates, and the lowest for C. epigejos substrates. The content of potassium does not differ statistically significantly in the substrates from sites dominated by D. carota and P. compressa. The highest values of Mg content were recorded for D. carota and were statistically different from Poa compressa sites, while the higher phosphorus content (statistically significantly different) was recorded for patches dominated by T. farfara and P. compressa.

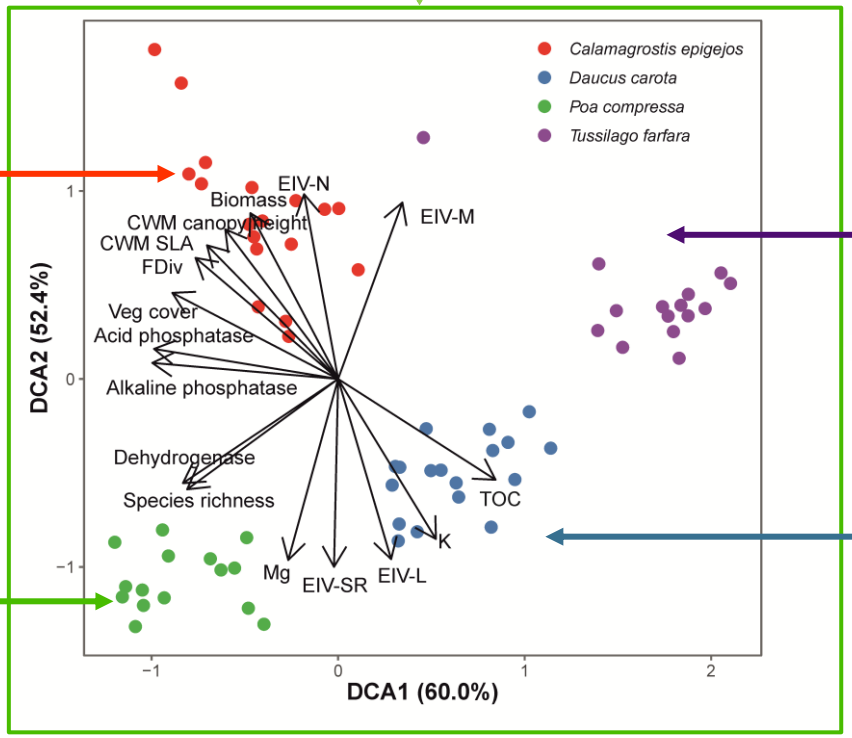
Despite our assumptions, the species with the highest mean biomass (Calamagrostis epigejos) did not cause lower species or functional diversity. In contrast, Tussilago farfara has the highest impact on postindustrial site habitats on coal mine heaps, as extreme values of four soil substratum parameters were recorded on these plots. This species also decreased both species and functional diversity of vegetation. The knowledge about relationship existing between plants (aboveground vegetation) and soil organisms seems important in order to undertake suitable reclamation measures and to restore variety of functions as well as to create diverse vegetation based on native species.

Graphical Abstract (for review)

DOMINANT SPECIES

vegetation composition ⇄ soil substratum

Calamagrostis epigejos



Tussilago farfara

Poa compressa

Daucus carota

Dominant species are differently shaping habitats of post-coal mining spoil heaps

Dominant species of higher biomass do not strongly influence species diversity and parameters of soil substratum

Research Highlights

Habitat shaping roles of dominant plant species on coal mine spoils was tested

Dominants with higher biomass do not always lower floristic and functional diversity

Dominants with higher biomass do not always seriously affect substrate properties

Effects of dominants on biological activity of spoil heap substrates were tested.

1. Introduction

Human influences on the environment are most often visible by shifts in vegetation composition (Bardgett and Wardle, 2010; Butchart et al., 2010; Waters et al., 2016). Many studies on this topic focus on analysing plant–soil interactions, the effects of plant species richness, plant productivity, as well as carbon and nitrogen capture (Balvanera et al., 2006; Hector and Bagchi, 2007; Markowicz et al., 2015). Among the issues that have been explored in terms of the vegetation diversity of degraded land are those connected with plant species evenness and identity of the dominant species. Vegetation patches in developing systems that emerge on habitats of novel ecosystems (Hobbs et al., 2006), such as post-industrial sites, provide an opportunity to study the relationships between the dominant plant species and the abiotic and biotic substrate (anthroposols) parameters along with species richness, functional diversity and biomass production of the developing vegetation. In novel ecosystems, some of the ecological relationships are established as a result of previously unknown processes caused by the extreme human impact on the Earth's ecosystems during the Anthropocene (Waters et al., 2016). Post-industrial sites provide a good example of newly established habitats which differ from the natural ecosystems in the surrounding landscape. Many studies have revealed that regardless of the degradation caused by industry, these sites have been colonized by living organisms through spontaneous succession, providing novel species compositions of flora and fauna (Hobbs et al., 2006; Kowarik, 2011). Differences in the chemical and physical properties of post-industrial substrates have resulted in unknown species compositions of the vegetation and animal organisms (Helingerová et al., 2010; Novák and Prach, 2003; Woźniak, 2010). The vegetation growing on coal mine spoil heaps consists of a mosaic of patches dominated by various species confined to a variety of microhabitats (Rawlik et al., 2018a; Rawlik et al., 2018b; Woźniak et al., 2015). On post-

industrial sites, including coal mine spoil heaps, it has been regularly observed that many unvegetated places still exist between the vegetation patches (Woźniak, 2010). Amongst the high diversity of vegetation types recorded at the early stages of successional development on coal mine spoil heaps, some of the vegetation types are particularly frequent. A few dominant grass species are very frequent, such as *Calamagrostis epigejos* and *Poa compressa*, and some very frequent herbaceous plants, including *Daucus carota* and *Tussilago farfara*, have been studied. The dominant plant species are accompanied by high plant species richness with differing cover abundances (Woźniak, 2010). The impacts of early-successional vegetation, or vegetation occurring on substrates of harsh site conditions, are less well known (Emery, 2007; Lamošová et al., 2010; Orwin et al., 2014; Peltzer et al., 2009), especially in novel ecosystems. Some research on dominant plant species has also been conducted on post-industrial sites (Prach and Pyšek, 1999; Woźniak, 2010) and these studies have mostly been focused on the species composition that accompanies the dominant plants on a range of different types of post-industrial sites.

We aimed to investigate the habitat-shaping role of the four main dominant species frequently occurring on coal-mine spoil heaps, expressed as their impact on the abiotic and biotic conditions of the substrate. Moreover, we wanted to assess the differences in the floristic and functional composition of accompanying species within early successional vegetation dominated by the most abundant species studied. We hypothesized that (1) the dominant species with higher mean biomass cause lower values for diversity indices than the other aboveground species in the vegetation; (2) the dominant species with higher mean biomass have a higher impact on belowground parameters in the substrate (e.g. enzyme activity, conductivity, nutrients).

2. Methods

2.1 Study area

The study sites are located in the area of Upper Silesia, Poland, in the Silesian Uplands. Earth and hard coal excavation has resulted in large amounts of wastes and land degradation. Collection of the waste has resulted in the creation of post-mining spoil heaps as the most frequent type of post-industrial waste sites (Prach et al., 2001). These coal mine spoil heaps, as human-created forms, are composed of carboniferous gangue together with sediments of Pre-Cambrian crystalline rocks (siltstone, sandstone, clay stone and conglomerates (Cabała et al., 2004).

Despite their harsh environments, these heaps can be spontaneously colonized by diverse herbaceous vegetation (Prach et al., 2013; Woźniak, 2010). The resulting vegetation can be scattered all over the heaps, resulting in a characteristic patchy spatial pattern. The vegetated places are interspersed with uncolonised bare ground which are unaffected by the vegetated areas and were locations of our control plots. A preliminary study of the spontaneous vegetation on these spoil heaps revealed that the vegetation is very diverse, but not all recorded vegetation types are equally frequent on the heaps, with some of the vegetation types being particularly frequent. Among the most frequent vegetation types are patches dominated by the grass species *Calamagrostis epigejos* and *Poa compressa* and the herbaceous species *Tussilago farfara* and *Daucus carota* (Table 1).

Table 1. Overview of species ecology, according to the BiolFlor database (Klotz et al., 2002), ecological indicator values (EIVs; Ellenberg and Leuschner, 2010) and LEDA functional traits database (Kleyer et al., 2008).

2.2 Vegetation sampling

Based on a preliminary study, a list of the most frequent vegetation types was prepared. The target vegetation types for this study (those dominated by *Calamagrostis epigejos, Poa compressa, Tussilago farfara, Daucus carota*) were selected by stratified sampling. We sampled four post-coal mining spoil heaps: "Sośnica" (50°16'22"N, 18°44'43"E), "Wesoła" (50°10'28"N, 19°5'44"E), "Maria" (50°11'19"N, 19°2'0"E) and "Kostuchna" (50°11'4"N, 19°0'33"E). These study sites are representative of numerous areas studied previously (Woźniak, 2010). Samples were collected from spontaneously developed herbaceous vegetation on these spoil heaps which were up to 30 years old.

Vegetation sampling plots were circular with a 3 m radius, and each plot was located in the middle of a homogeneous vegetation patch. The vascular plant species composition with their abundances (visually estimated as cover of all individuals of recorded species) were recorded for each sampling plot. In total, 83 spoil samples were collected (67 in vegetation plots and 16 in control sites not covered by vegetation).

2.3 Substrate sampling

In each plot spoil material was collected from five evenly distributed locations (including the middle and four distant places of each plot, with a 10 cm diameter soil coring device to a depth of 10-15 cm and then bulked into one composite sample for analysis of physical, chemical and soil enzyme activity parameters. Within the vegetation patches, individual plants of the four species were gently pulled out and shaken to obtain spoil material from the root zone. Soil pH and electrical conductivity (EC) were measured in water suspension (Bednarek et al., 2004).

The Tiurin method was applied to assess the total carbon content (TOC) (Bednarek et al., 2004). Total N (TN) was determined by the Kjeldahl method (Rutherford et al.2007). The analysis of available phosphorus contents was based on the Egner-Riehm method (PN-R-

04023:1996). The content of available K, Na and Mg was measured by spectrometric analysis (Ostrowska et al., 1991).

2.4 Above-ground biomass

The biomass was assessed by applying the following procedures: in each vegetation plot above-ground plant biomass was harvested in a representative 0.5 x 0.5 m subsample. Subsamples were taken, avoiding areas where plants were pulled out for root zone substrate samples. Biomass of the dominant plant species was separated from the biomass of the accompanying plant species. The weight of fresh biomass was measured in the field as soon as the sample was collected. The weight of both subsamples of fresh biomass was recorded. All the biomass samples were subsequently dried in an incubator at 105°C for 24 hours and the dry weight of the samples was determined in the laboratory. We checked after 24 h of drying that the mass of the samples was constant.

2.5 Enzyme assays

Dehydrogenase [EC 1.1] activities in the coal mine spoil substrate were determined by reduction of 2,3,5-triphenyltetrazolium chloride (TTC) to triphenylformazan (TPF) by the method developed by Schinner et al. (1996). The activity of urease [EC 3.5.1.5] was determined by a modified Hoffmann and Teicher (1961) method. Acid [EC 3.1.3.2] and alkaline phosphatase [EC 3.1.3.1] activity, were determined by measuring the p-nitrophenol (PNP) released by the phosphatase activity.

2.6 Functional diversity

The analysed traits of our four dominant species were extracted from the LEDA Traitbase (Kleyer et al., 2008). The recorded plant species were characterized by selected

traits (Table 1). For each plot we calculated community-weighted mean values (CWM) of these traits, as well as functional diversity indices: functional richness, divergence and dispersion as components of functional diversity (Laliberté and Legendre 2010; Mason et al., 2005). The values of functional diversity indices reflect the main processes shaping a plant community such as competition and environmental filtering (Bu et al., 2014; Czortek et al., 2018; Dyderski et al., 2016). Functional diversity and CWMs were calculated using the *FD::dbFD()* function (Laliberté et al., 2014).

2.7 Data analyses

To explore relationships between vegetation species composition and environmental factors we conducted Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980). This analysis works well for data representing long ecological gradients. In the DCA algorithm, species and site scores are scaled in units of standard deviation to overcome the problems with packing observations in the middle of the ordination space. We used an algorithm implemented in the *vegan::decorana()* function (Oksanen et al., 2016). To assess the indirect relationships between species composition and environmental variables we used a passive projection of vectors which increased with increasing trait values. This projection was implemented in the *vegan::envfit()* function (Oksanen et al., 2016). To compare groups we used one-way analysis of variance (ANOVA) followed by Tukey's *posteriori* test. All mean values are followed by their standard error (SE), as a dispersion measure. We did not adjust p values from multiple tests (e.g. by Bonferroni correction), assuming the argument given by Moran (2003), to not omit possibly important results.

All analyses were conducted using R software (R Core Team 2018).

3. Results

The DCA analysis revealed four main groups of factors determining the distribution of vegetation patches along the environmental gradients. The DCA1 and DCA2 axes explained 60% and 52 % of the variability, respectively. The DCA (**Table 1**) revealed a clear distinction between the patches dominated by the four analyzed vegetation types. All of them were nicely clustered in different parts of the scatter plot, thus indicating different gradients. Apart from the patches dominated by *Tussilago farfara* all of the other patch types were correlated with biotic and abiotic environmental factors (**Fig. 1**).

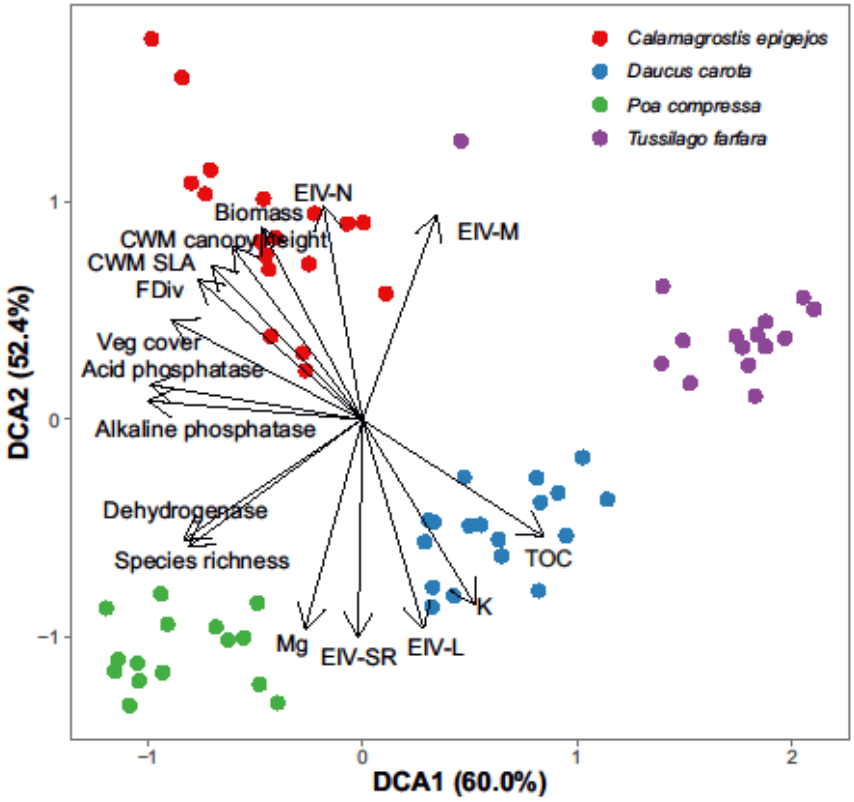


Fig. 1. Detrended correspondence analysis of vegetation in plots dominated by the species studied. Arrows are vectors representing parameters described in **Table A1.** Only parameters statistically significantly ($p<0.05$) correlated with DCA scores are shown.

The occurrence of the vegetation patches dominated by *Calamagrostis epigejos* was correlated with parameters such as amount of biomass, canopy height CWM and specific leaf area CWM. Vegetation patches dominated by *Daucus carota* were grouped in the bottom right corner of the DCA graph. These patches were related to the light requirements (EIV-L), Total Organic Carbon (TOC) and potassium content. The vegetation patches dominated by *Poa compressa* were related to dehydrogenase activity, higher magnesium content and species richness of the vegetation patches. The vegetation patches dominated by *Tussilago farfara* seemed to be most related to the first axis and its associated gradient located opposite to the gradient described by the activity of all the soil enzymes studied.

The comparison of some parameters of rhizosphere substrate samples from under the dominant plant species in the vegetation patches of *Calamagrostis epigejos, Daucus carota, Tussilago farfara,* and *Poa compressa* (**Table 1**) revealed differences in (TOC). The highest TOC content was recorded for *T. farfara* substrates, and the lowest for *C. epigejos* substrates. The content of potassium did not differ statistically significantly in the substrates from sites dominated by *D. carota* and *P. compressa*. The rhizosphere soil substrate in patches dominated by *D. carota* and *P. compressa* were statistically significantly different in Mg content, with the highest values recorded for *D. carota.* The higher phosphorus contents (statistically significantly different) were recorded for patches dominated by *T. farfara* and *P. compressa* (**Table 2**).

Table 2. Mean and SE of soil parameters for plots dominated by the species studied and plots without vegetation. Groups marked by the same letter in a row do not differ statistically significantly at p=0.05, according to Tukey's *posteriori* test. The highest value is indicated in bold.

Regarding the biotic substrate parameters (soil enzymes), dehydrogenase activity was not statistically significantly different for patches dominated by *C. epigejos*, *D. carota* and *T. farfara*, but was statistically significantly higher in patches dominated by *P. compressa*. The activity of acid phosphatase was statistically significantly higher in patches dominated by *C. epigejos* and statistically different from patches dominated by *D. carota* and *T. farfara*, while the activity of alkaline phosphatase was statistically significantly higher in patches dominated by *P. compressa* and statistically significantly different from patches dominated by *T. farfara*. The urease content in the substrate of vegetation plots did not have any statistically significant differences (**Table 3**). The results revealed no statistically significant differences in the values for pH in KCl, pH in H_2O, conductivity, nitrogen and sodium content (**Table 2**).

Table 3. Mean and SE of vegetation parameters for plots dominated by the species studied and plots without vegetation. Groups marked by the same letter in a row do not differ statistically significantly at p=0.05, according to Tukey's *posteriori* test. The highest value is indicated in bold.

The biomasses were statistically significantly different among patches dominated by the four species and were highest for *C. epigejos* patches (**Table 3**). Vegetation cover was significantly different and was highest in patches dominated by *C. epigejos* and *P. compressa*. Species richness was significantly lower in patches dominated by *T. farfara*. The highest CWM canopy height was recorded for vegetation dominated by *C. epigejos* and was significantly different from both *D. carota* and *P. compressa* as well as *T. farfara*. The CWM of specific leaf area was significantly higher in patches dominated by *C. epigejos*. In patches dominated by *C. epigejos* the functional richness and divergence were statistically significantly higher than in patches dominated by *T. farfara*. The vegetation patches

dominated by *P. compressa* were characterized by a species composition with higher light requirements (EIV-L) and were significantly different from both *D. carota* and *C. epigejos* as well as *T. farfara*. All the studied vegetation patches differed statistically significantly from each other in terms of moisture requirements (EIV-M). The species composition of vegetation patches dominated by *C. epigejos* suggests statistically higher requirements for nitrogen (EIV-N) in the soil substrate and is statistically significantly different from the vegetation patches dominated by *T. farfara* and *P. compressa*. In terms of the requirements for soil substrate reaction (EIV-SR) the patches dominated by *T. farfara* and *P. compressa* have significantly higher requirements compared to patches dominated by *C. epigejos* and *D. carota*.

4. Discussion

Coal mine spoil heaps are recognized as heterogeneous habitats with unusual and extreme abiotic and biotic conditions and low productivity (Tropek et al., 2012; Woźniak, 2010). Spoil heaps provide harsh environments, but despite their anthropogenic origin, the substrate from which heaps are built does not contain high concentrations of heavy metals and toxins, which could inhibit the growth of plants (Woźniak 2010; Stefanowicz et al. 2015; Kompała-Bąba et al. 2019). Our earlier studies (data not published) also showed relatively low concentrations of bioavailable forms of metals such as Cd (0.02-0.13 mg kg^{-1} d.m.), Pb (0.07-0.15 mg kg^{-1} d.m.) and Zn (0.15-6.14 mg kg^{-1} d.m.) on the spoil heaps analysed in the studies presented herein. Pietrzykowski et al. (2014), based on the heavy metal content in substrate and *Pinus sylvestris* needles, found that there is no risk of critical levels and bioavailability of heavy metals in the substrate in hard-coal heaps. Moreover, Dang et al. (2002) indicated that during the natural weathering of coal mine spoil heaps, only a small

fraction of heavy metals that may occur in the waste are released to the environment, with most of them remaining in the residual material.

Spoil heaps –provide compensatory habitats in the modern human-altered landscape (Skalski et al., 2016). The significant influence of vegetation type (species and functional composition) on soil chemical and physical properties is well known from natural and semi-natural sites (Wilson et al., 2012 and literature cited therein). Plant productivity, or biomass, has been considered by some authors to be basic ecosystem characteristics (Laughlin, 2011; McLaren and Turkington, 2010). Abundance of plants has a preliminary influence on the quantity of exudates and plant remnants the soil receives (Bastida et al., 2008a; Bastida et al., 2008b). Other studies have used, among others, the soil carbon and nitrogen contents to assess the quality of ecosystem functioning (Mokany et al., 2006). Attempting to understand how the dominant species, with higher mean biomass, influence vegetation diversity and below ground parameters in the substrate is one of the possible approaches to understand development of a post-industrial ecosystem (Markowicz et al., 2015). Ecosystem functioning is related to the specificity of habitats of the newly developing ecosystem (Costanza et al., 1997; Kompała-Bąba et al. 2019). Differences in the amount of biomass recorded among the vegetation patches analysed (different dominant plant species) suggests the variety of ways in which particular vegetation patches influence the processes of development of post-industrial ecosystem functioning (Piekarska-Stachowiak et al., 2014; Stefanowicz et al., 2015).

In contrast to post-industrial areas, natural and semi-natural habitats are well recognized in terms of relationships between biomass production and biodiversity, as well as their role in shaping ecosystem functioning (Liang et al., 2016). However, most of the studies on plant species diversity were not related to the soil (Pereira et al., 2010; Tropek et al., 2017; Wilson et al., 2012). Our study revealed how the dominant plant species shape complex and highly variable relationships between the functional diversity of the vegetation associated

with the dominant species and soil substratum (abiotic and biotic), in terms of their habitat-shaping (above ground and below ground) parameters on human-created, post-industrial coal mine spoil heaps. These relationships reflect similar patterns known from natural and semi-natural ecosystems. Our study revealed that the highest species richness occurred in vegetation patches dominated by *Poa compressa*. However, this species does not achieve the highest biomass among the dominant species studied. In patches dominated by *Calamagrostis epigejos* values of vegetation cover, CWMs of specific leaf area and canopy height were significantly higher. This corresponds with the theory of biodiversity-productivity relationships, which indicates that the highest species diversity will be in the region with intermediate productivity (Mittelbach et al., 2001; Tilman, 1999; Wilson et al., 2012). Thus, differences in ecological requirements of the dominant species determine spatial heterogeneity and gamma diversity of post-industrial areas (Piekarska-Stachowiak et al., 2014).

The effects of dominant species on ecosystem functioning have been better described in reclaimed forests (e.g. Horodecki and Jagodziński, 2017; Rawlik et al., 2018b). The impacts of dominants are mostly manifested in the soil chemistry and understory species composition, due to the different elemental contents of tree biomass and the high biomass of trees, in contrast to the herbaceous species studied. For example, Rawlik et al. (2018b) found differences in soil P, K, Mg, Ca and Fe contents among stands of five dominant tree species. In our previous studies we also detected the effects of some dominant species on physicochemical soil parameters (Stefanowicz et al. 2015).

Contrary to our expectations, the species richness and functional diversity parameters were not lowest in patches dominated by the expansive grass *Calamagrostis epigejos*. Species richness was highest in patches dominated by *Poa compressa*. Surprisingly, functional divergence and functional richness were significantly higher in patches dominated by

Calamagrostis epigejos and were lowest in patches dominated by *Tussilago farfara*. High functional divergence in a vegetation patch indicates a high level of niche differentiation, and thus competition for different resources (low selection by environmental filtering) (Kraft et al., 2015). Thus, vegetation assemblages with high functional divergence may have increased ecosystem functioning as a result of higher effective resource utilization (de Bello et al., 2013; Podani et al., 2013). High functional richness and divergence are indicators of low environmental filtering (Laliberté and Legendre, 2010). However, in our previous studies we did not find any support for these two indices as indicators of harsher habitats (Czortek et al., 2018; Dyderski et al., 2017). In the studied system we may assume that higher functional divergence and functional richness in *Calamagrostis epigejos* may be an effect of the stronger dominance of this species. The other species occurring in patches dominated by *Calamagrostis epigejois* were usually a random admixture, representing various guilds, but which were never able to increase their contribution to the plant community. Thus, their different traits extended the community volume within the trait hyperspace.

In our study the amount of magnesium (Mg) was significantly higher under the vegetation patches dominated by *Daucus carota*, while the lowest amount of Mg was recorded under vegetation patches dominated by *Tussilago farfara*. Due to its unique chemistry, Mg is subject to various cycling processes within ecosystems. The important role of magnesium is connected with its high mobility (Cakmak and Yazici, 2010; Karley and White, 2009). In this respect the vegetation type, and its species composition, is very important in newly developing post-industrial ecosystems (Bose et al., 2011; Shaul, 2002). Magnesium plays an important role in increasing a plant's tolerance to various stresses, which influences its biomass (Gransee and Führs, 2013). The soil property found to be the most clearly influenced by different species was organic carbon (TOC). Contrary to our expectations it was highest in patches dominated by *Tussilago farfara*. In our study the

dominant species *Tussilago farfara* did not achieve the highest biomass, but this species had the highest leaf mass and leaf area. It also prefers soils with a high clay content, which are usually fertile and rich in organic matter (Namura-Ochalska, 1993). On coal-mine spoil heaps patches with *Tussilago farfara* are confined to gravelly, sandy or stony substrates (Kompała-Bąba et al. 2019).

The highest potassium (K) content was found in the substrate taken from ~~under~~ vegetation patches dominated by *Tussilago farfara.* The K content was lowest in the vegetated plots dominated by the species with the lowest biomass, *Daucus carota.* It has been stated that the optimal potassium (K+): sodium (Na+) ratio is vital to activate enzymatic reactions in plants (Wakeel, 2013). Although most soils have adequate amounts of K+, in many soils the available K+ has become insufficient (Wakeel, 2013). The balance of elements on post-industrial sites depends on the mineral composition of stones and rocks which have been randomly gathered into coal mine spoil heaps. The habitat-shaping role of spontaneous vegetation in such cases is particularly important.

In many studies sodium (Na+) is reported as a toxic ion which affects plant growth by its detrimental influence on plant metabolism in inhibiting enzyme activities (Wakeel, 2013). It is reported that the available K+ can become insufficient in many sites (Mishra et al., 2015). The deficiency of K content is exacerbated partially as a consequence of K to Na antagonism. This is interesting, as in coal mine post-industrial sites the amount of potassium is significantly higher under the vegetation patches dominated by *Tussilago farfara* and *Poa compressa,* but no differences in the amount of Na+ and conductivity were recorded under any of the studied vegetation types. This is important considering that K+ uptake by plants is severely affected by the presence of Na+ in the nutrient medium (Mishra et al., 2015).

We also found the highest P content under the vegetation patches dominated by *Tussilago farfara*. The plant phosphorus concentrations and its SOM input depend on many

factors including soil parameters (coal mine spoil heap soil substrate) and plant growth form (Chen et al., 2018; Tang et al., 2018).

In terms of abiotic parameters, the presence of vegetation did not influence the conductivity and sodium content in the substrate on the surface of the coal mine spoil heaps. These results confirmed our previous findings where we did not find differences of electrical conductivity among vegetation plots with different dominant species, but electrical conductivity decreased with time as soluble salts were leached from the upper soil layers. Surprisingly, the presence of vegetation did not influence the total nitrogen content. Other studies conducted on coal mine spoil heaps and also other post-industrial sites have reported that generally nitrogen is below the detectable level. It has been stated that the presence of vegetation influences the value of surface pH on coal mine spoil heaps. In our previous studies substrate pH hardly differed among vegetation types (dominated by *Tussilago farfara*, *Calamagrostis epigejos* or *Chamaenerion palustre*), between plots with or without vegetation, or among spoil heaps of different ages. It ranged over 1.5 to 4 pH units (Stefanowicz et al. 2015). According to the ‘‘diversity hypothesis’’ the more diverse a given community is, then the higher resource utilization by species possessing different functional traits is, because of lower niche overlap (Tilman et al., 1997). Therefore, diverse communities influence ecosystem functioning because the entire pool of available resources is increased (Díaz and Cabido, 2001; Rao, 1982; Ricotta and Moretti, 2011). This is highly visible in natural and semi-natural plant communities (Grime and Mackey, 2002; Li et al., 2018; Loreau et al., 2002). The ‘mass ratio hypothesis’ explains that ecosystem functioning is mainly dominated by the traits of a dominant species (Grime et al., 1988). The more abundant species utilize a greater proportion of resources, thus the dominant species contribute disproportionately to ecosystem functioning (Cadotte et al., 2011). In contrast, the species with low abundances are relatively less important (Laughlin, 2011).

Our results have revealed the superior role of dominant plant species in the recovery of post-industrial sites. We found that the studied vegetation types significantly influenced the biological activity of coal mine spoil heaps. Dehydrogenase and alkaline phosphatase activity was highest under the patches dominated by *Poa compressa,* whereas acid phosphatase activity was highest under the patches dominated by *Calamagrostis epigejos*. These effects may be used to accelerate reclamation processes and may help to predict the course of reclamation on areas left to spontaneous succession. This may be related to the fact that the grasses have a well-developed root system (De Baets et al., 2006), which is associated with the secretion of large amounts of root exudates (Bąba et al., 2016; Mommer et al., 2010; Ravenek et al., 2014). A large number of fine roots and their exudates stimulate the development of arbuscular mycorrhizal fungi (AMF) and other microorganisms, largely responsible for the activity of soil dehydrogenase (Wolińska and Stępniewska, 2012). In addition, the roots of plants and AMF have been proven to be the main source of acid phosphatase in the soil, while the bacteria mainly produce alkaline phosphatase (Sakurai et al., 2008).

Our study has provided comprehensive evidence that dominant species in the spontaneous vegetation developing on post-industrial sites alter its species and functional composition, as well as the chemical and biological properties of the soil substrate. Despite our assumptions (Hypothesis 1), the species with the highest mean biomass (*Calamagrostis epigejos*) did not cause lower species or functional divergence in its vegetation patches than e.g. *Tussilago farfara*, that had the second highest mean biomass. We also found that as a dominant plant, *Tussilago farfara* seemed to have the highest impact on the habitats formed on post-industrial coal mine spoil heaps, compared to the other species studied. This contradicts hypothesis 2, which assumed the highest impact by *Calamagrostis epigejos*. Four of the soil substratum parameters (TOC, P, K, N) were recorded at their highest levels under

vegetation patches dominated by *Tussilago farfara*. This suggests that the habitat-shaping role of *Tussilago farfara* is considerable, regardless of the fact that the species number and functional divergence was lowest in *Tussilago farfara* dominated patches and that the biomass of these patches was intermediate.

Conclusions

The relationship between the vegetation types studied did not always follow the known rules for natural or semi-natural vegetation. The results indicated that developing novel ecosystems are not well understood and require further study; otherwise, reclamation and restoration processes will be insufficient or will fail. Dominant species utilize existing resources on post-industrial sites in different ways and they also influence both aboveground and belowground species and functional diversity in different ways. Obtaining knowledge about relationships existing between plants (aboveground vegetation) and soil organisms seems extremely important to undertake suitable reclamation or restoration measures, to restore a variety of ecosystem functions, and to create diverse vegetation based mainly on native species.

There is no conflict of interest concerning this paper.

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1. Introduction

Human influences on the environment are most often visible by shifts in vegetation composition (Bardgett and Wardle, 2010; Butchart et al., 2010; Waters et al., 2016). Many studies on this topic focus on analysing plant–soil interactions, the effects of plant species richness, plant productivity, as well as carbon and nitrogen capture (Balvanera et al., 2006; Hector and Bagchi, 2007; Markowicz et al., 2015). Among the issues that have been explored in terms of the vegetation diversity of degraded land are those connected with plant species evenness and identity of the dominant species. Vegetation patches in developing systems that emerge on habitats of novel ecosystems (Hobbs et al., 2006), such as post-industrial sites, provide an opportunity to study the relationships between the dominant plant species and the abiotic and biotic substrate (anthroposols) parameters along with species richness, functional diversity and biomass production of the developing vegetation. In novel ecosystems, some of the ecological relationships are established as a result of previously unknown processes caused by the extreme human impact on the Earth's ecosystems during the Anthropocene (Waters et al., 2016). Post-industrial sites provide a good example of newly established habitats which differ from the natural ecosystems in the surrounding landscape. Many studies have revealed that regardless of the degradation caused by industry, these sites have been colonized by living organisms through spontaneous succession, providing novel species compositions of flora and fauna (Hobbs et al., 2006; Kowarik, 2011). Differences in the chemical and physical properties of post-industrial substrates have resulted in unknown species compositions of the vegetation and animal organisms (Helingerová et al., 2010; Novák and Prach, 2003; Woźniak, 2010). The vegetation growing on coal mine spoil heaps consists of a mosaic of patches dominated by various species confined to a variety of microhabitats (Rawlik et al., 2018a; Rawlik et al., 2018b; Woźniak et al., 2015). On post-

industrial sites, including coal mine spoil heaps, it has been regularly observed that many unvegetated places still exist between the vegetation patches (Woźniak, 2010). Amongst the high diversity of vegetation types recorded at the early stages of successional development on coal mine spoil heaps, some of the vegetation types are particularly frequent. A few dominant grass species are very frequent, such as *Calamagrostis epigejos* and *Poa compressa*, and some very frequent herbaceous plants, including *Daucus carota* and *Tussilago farfara*, have been studied. The dominant plant species are accompanied by high plant species richness with differing cover abundances (Woźniak, 2010). The impacts of early-successional vegetation, or vegetation occurring on substrates of harsh site conditions, are less well known (Emery, 2007; Lamošová et al., 2010; Orwin et al., 2014; Peltzer et al., 2009), especially in novel ecosystems. Some research on dominant plant species has also been conducted on post-industrial sites (Prach and Pyšek, 1999; Woźniak, 2010) and these studies have mostly been focused on the species composition that accompanies the dominant plants on a range of different types of post-industrial sites.

We aimed to investigate the habitat-shaping role of the four main dominant species frequently occurring on coal-mine spoil heaps, expressed as their impact on the abiotic and biotic conditions of the substrate. Moreover, we wanted to assess the differences in the floristic and functional composition of accompanying species within early successional vegetation dominated by the most abundant species studied. We hypothesized that (1) the dominant species with higher mean biomass cause lower values for diversity indices than the other aboveground species in the vegetation; (2) the dominant species with higher mean biomass have a higher impact on belowground parameters in the substrate (e.g. enzyme activity, conductivity, nutrients).

2. Methods

2.1 Study area

The study sites are located in the area of Upper Silesia, Poland, in the Silesian Uplands. Earth and hard coal excavation has resulted in large amounts of wastes and land degradation. Collection of the waste has resulted in the creation of post-mining spoil heaps as the most frequent type of post-industrial waste sites (Prach et al., 2001). These coal mine spoil heaps, as human-created forms, are composed of carboniferous gangue together with sediments of Pre-Cambrian crystalline rocks (siltstone, sandstone, clay stone and conglomerates (Cabała et al., 2004).

Despite their harsh environments, these heaps can be spontaneously colonized by diverse herbaceous vegetation (Prach et al., 2013; Woźniak, 2010). The resulting vegetation can be scattered all over the heaps, resulting in a characteristic patchy spatial pattern. The vegetated places are interspersed with uncolonised bare ground which are unaffected by the vegetated areas and were locations of our control plots. A preliminary study of the spontaneous vegetation on these spoil heaps revealed that the vegetation is very diverse, but not all recorded vegetation types are equally frequent on the heaps, with some of the vegetation types being particularly frequent. Among the most frequent vegetation types are patches dominated by the grass species *Calamagrostis epigejos* and *Poa compressa* and the herbaceous species *Tussilago farfara* and *Daucus carota* (Table 1).

Table 1. Overview of species ecology, according to the BiolFlor database (Klotz et al., 2002), ecological indicator values (EIVs; Ellenberg and Leuschner, 2010) and LEDA functional traits database (Kleyer et al., 2008).

2.2 Vegetation sampling

Based on a preliminary study, a list of the most frequent vegetation types was prepared. The target vegetation types for this study (those dominated by *Calamagrostis epigejos, Poa compressa, Tussilago farfara, Daucus carota*) were selected by stratified sampling. We sampled four post-coal mining spoil heaps: "Sośnica" (50°16'22"N, 18°44'43"E), "Wesoła" (50°10'28"N, 19°5'44"E), "Maria" (50°11'19"N, 19°2'0"E) and "Kostuchna" (50°11'4"N, 19°0'33"E). These study sites are representative of numerous areas studied previously (Woźniak, 2010). Samples were collected from spontaneously developed herbaceous vegetation on these spoil heaps which were up to 30 years old.

Vegetation sampling plots were circular with a 3 m radius, and each plot was located in the middle of a homogeneous vegetation patch. The vascular plant species composition with their abundances (visually estimated as cover of all individuals of recorded species) were recorded for each sampling plot. In total, 83 spoil samples were collected (67 in vegetation plots and 16 in control sites not covered by vegetation).

2.3 Substrate sampling

In each plot spoil material was collected from five evenly distributed locations (including the middle and four distant places of each plot, with a 10 cm diameter soil coring device to a depth of 10-15 cm and then bulked into one composite sample for analysis of physical, chemical and soil enzyme activity parameters. Within the vegetation patches, individual plants of the four species were gently pulled out and shaken to obtain spoil material from the root zone. Soil pH and electrical conductivity (EC) were measured in water suspension (Bednarek et al., 2004).

The Tiurin method was applied to assess the total carbon content (TOC) (Bednarek et al., 2004). Total N (TN) was determined by the Kjeldahl method (Rutherford et al.2007). The analysis of available phosphorus contents was based on the Egner-Riehm method (PN-R-

04023:1996). The content of available K, Na and Mg was measured by spectrometric analysis (Ostrowska et al., 1991).

2.4 Above-ground biomass

The biomass was assessed by applying the following procedures: in each vegetation plot above-ground plant biomass was harvested in a representative 0.5 x 0.5 m subsample. Subsamples were taken, avoiding areas where plants were pulled out for root zone substrate samples. Biomass of the dominant plant species was separated from the biomass of the accompanying plant species. The weight of fresh biomass was measured in the field as soon as the sample was collected. The weight of both subsamples of fresh biomass was recorded. All the biomass samples were subsequently dried in an incubator at 105°C for 24 hours and the dry weight of the samples was determined in the laboratory. We checked after 24 h of drying that the mass of the samples was constant.

2.5 Enzyme assays

Dehydrogenase [EC 1.1] activities in the coal mine spoil substrate were determined by reduction of 2,3,5-triphenyltetrazolium chloride (TTC) to triphenylformazan (TPF) by the method developed by Schinner et al. (1996). The activity of urease [EC 3.5.1.5] was determined by a modified Hoffmann and Teicher (1961) method. Acid [EC 3.1.3.2] and alkaline phosphatase [EC 3.1.3.1] activity, were determined by measuring the p-nitrophenol (PNP) released by the phosphatase activity.

2.6 Functional diversity

The analysed traits of our four dominant species were extracted from the LEDA Traitbase (Kleyer et al., 2008). The recorded plant species were characterized by selected

traits (Table 1). For each plot we calculated community-weighted mean values (CWM) of these traits, as well as functional diversity indices: functional richness, divergence and dispersion as components of functional diversity (Laliberté and Legendre 2010; Mason et al., 2005). The values of functional diversity indices reflect the main processes shaping a plant community such as competition and environmental filtering (Bu et al., 2014; Czortek et al., 2018; Dyderski et al., 2016). Functional diversity and CWMs were calculated using the *FD::dbFD()* function (Laliberté et al., 2014).

2.7 Data analyses

To explore relationships between vegetation species composition and environmental factors we conducted Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980). This analysis works well for data representing long ecological gradients. In the DCA algorithm, species and site scores are scaled in units of standard deviation to overcome the problems with packing observations in the middle of the ordination space. We used an algorithm implemented in the *vegan::decorana()* function (Oksanen et al., 2016). To assess the indirect relationships between species composition and environmental variables we used a passive projection of vectors which increased with increasing trait values. This projection was implemented in the *vegan::envfit()* function (Oksanen et al., 2016). To compare groups we used one-way analysis of variance (ANOVA) followed by Tukey's *posteriori* test. All mean values are followed by their standard error (SE), as a dispersion measure. We did not adjust p values from multiple tests (e.g. by Bonferroni correction), assuming the argument given by Moran (2003), to not omit possibly important results.

All analyses were conducted using R software (R Core Team 2018).

3. Results

The DCA analysis revealed four main groups of factors determining the distribution of vegetation patches along the environmental gradients. The DCA1 and DCA2 axes explained 60% and 52 % of the variability, respectively. The DCA (**Table 1**) revealed a clear distinction between the patches dominated by the four analyzed vegetation types. All of them were nicely clustered in different parts of the scatter plot, thus indicating different gradients. Apart from the patches dominated by *Tussilago farfara* all of the other patch types were correlated with biotic and abiotic environmental factors (**Fig. 1**).

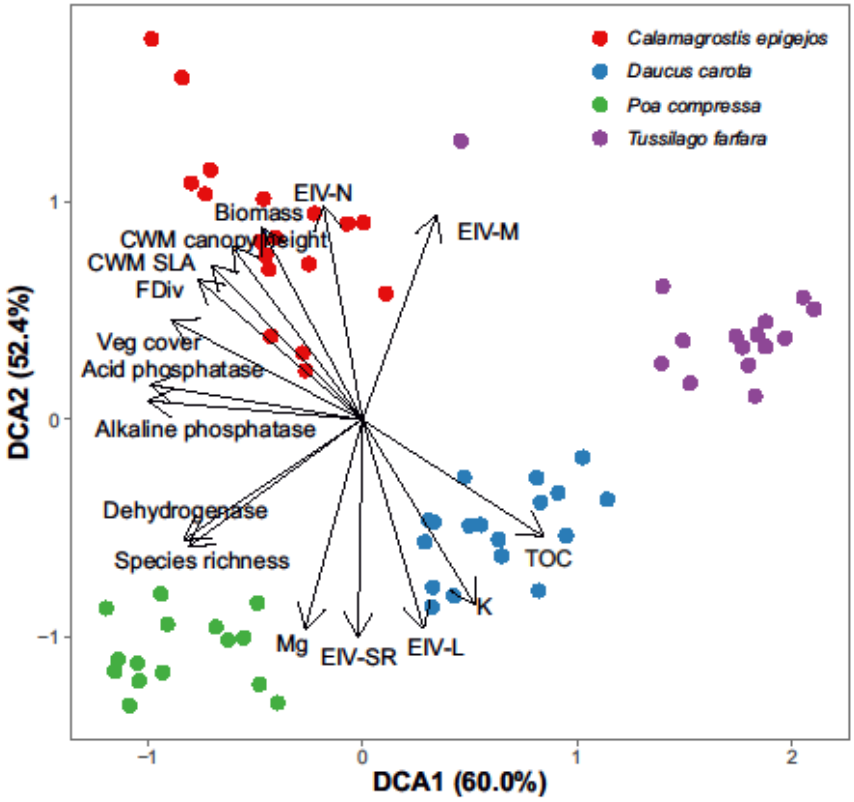

Fig. 1. Detrended correspondence analysis of vegetation in plots dominated by the species studied. Arrows are vectors representing parameters described in **Table A1.** Only parameters statistically significantly ($p<0.05$) correlated with DCA scores are shown.

The occurrence of the vegetation patches dominated by *Calamagrostis epigejos* was correlated with parameters such as amount of biomass, canopy height CWM and specific leaf area CWM. Vegetation patches dominated by *Daucus carota* were grouped in the bottom right corner of the DCA graph. These patches were related to the light requirements (EIV-L), Total Organic Carbon (TOC) and potassium content. The vegetation patches dominated by *Poa compressa* were related to dehydrogenase activity, higher magnesium content and species richness of the vegetation patches. The vegetation patches dominated by *Tussilago farfara* seemed to be most related to the first axis and its associated gradient located opposite to the gradient described by the activity of all the soil enzymes studied.

The comparison of some parameters of rhizosphere substrate samples from under the dominant plant species in the vegetation patches of *Calamagrostis epigejos, Daucus carota, Tussilago farfara,* and *Poa compressa* (**Table 1**) revealed differences in (TOC). The highest TOC content was recorded for *T. farfara* substrates, and the lowest for *C. epigejos* substrates. The content of potassium did not differ statistically significantly in the substrates from sites dominated by *D. carota* and *P. compressa*. The rhizosphere soil substrate in patches dominated by *D. carota* and *P. compressa* were statistically significantly different in Mg content, with the highest values recorded for *D. carota.* The higher phosphorus contents (statistically significantly different) were recorded for patches dominated by *T. farfara* and *P. compressa* (**Table 2**).

Table 2. Mean and SE of soil parameters for plots dominated by the species studied and plots without vegetation. Groups marked by the same letter in a row do not differ statistically significantly at p=0.05, according to Tukey's *posteriori* test. The highest value is indicated in bold.

Regarding the biotic substrate parameters (soil enzymes), dehydrogenase activity was not statistically significantly different for patches dominated by *C. epigejos*, *D. carota* and *T. farfara*, but was statistically significantly higher in patches dominated by *P. compressa*. The activity of acid phosphatase was statistically significantly higher in patches dominated by *C. epigejos* and statistically different from patches dominated by *D. carota* and *T. farfara*, while the activity of alkaline phosphatase was statistically significantly higher in patches dominated by *P. compressa* and statistically significantly different from patches dominated by *T. farfara*. The urease content in the substrate of vegetation plots did not have any statistically significant differences (**Table 3**). The results revealed no statistically significant differences in the values for pH in KCl, pH in H_2O, conductivity, nitrogen and sodium content (**Table 2**).

Table 3. Mean and SE of vegetation parameters for plots dominated by the species studied and plots without vegetation. Groups marked by the same letter in a row do not differ statistically significantly at p=0.05, according to Tukey's *posteriori* test. The highest value is indicated in bold.

The biomasses were statistically significantly different among patches dominated by the four species and were highest for *C. epigejos* patches (**Table 3**). Vegetation cover was significantly different and was highest in patches dominated by *C. epigejos* and *P. compressa*. Species richness was significantly lower in patches dominated by *T. farfara*. The highest CWM canopy height was recorded for vegetation dominated by *C. epigejos* and was significantly different from both *D. carota* and *P. compressa* as well as *T. farfara*. The CWM of specific leaf area was significantly higher in patches dominated by *C. epigejos*. In patches dominated by *C. epigejos* the functional richness and divergence were statistically significantly higher than in patches dominated by *T. farfara*. The vegetation patches

dominated by *P. compressa* were characterized by a species composition with higher light requirements (EIV-L) and were significantly different from both *D. carota* and *C. epigejos* as well as *T. farfara*. All the studied vegetation patches differed statistically significantly from each other in terms of moisture requirements (EIV-M). The species composition of vegetation patches dominated by *C. epigejos* suggests statistically higher requirements for nitrogen (EIV-N) in the soil substrate and is statistically significantly different from the vegetation patches dominated by *T. farfara* and *P. compressa*. In terms of the requirements for soil substrate reaction (EIV-SR) the patches dominated by *T. farfara* and *P. compressa* have significantly higher requirements compared to patches dominated by *C. epigejos* and *D. carota*.

4. Discussion

Coal mine spoil heaps are recognized as heterogeneous habitats with unusual and extreme abiotic and biotic conditions and low productivity (Tropek et al., 2012; Woźniak, 2010). Spoil heaps provide harsh environments, but despite their anthropogenic origin, the substrate from which heaps are built does not contain high concentrations of heavy metals and toxins, which could inhibit the growth of plants (Woźniak 2010; Stefanowicz et al. 2015; Kompała-Bąba et al. 2019). Our earlier studies (data not published) also showed relatively low concentrations of bioavailable forms of metals such as Cd (0.02-0.13 mg kg^{-1} d.m.), Pb (0.07-0.15 mg kg^{-1} d.m.) and Zn (0.15-6.14 mg kg^{-1} d.m.) on the spoil heaps analysed in the studies presented herein. Pietrzykowski et al. (2014), based on the heavy metal content in substrate and *Pinus sylvestris* needles, found that there is no risk of critical levels and bioavailability of heavy metals in the substrate in hard-coal heaps. Moreover, Dang et al. (2002) indicated that during the natural weathering of coal mine spoil heaps, only a small

fraction of heavy metals that may occur in the waste are released to the environment, with most of them remaining in the residual material.

Spoil heaps–provide compensatory habitats in the modern human-altered landscape (Skalski et al., 2016). The significant influence of vegetation type (species and functional composition) on soil chemical and physical properties is well known from natural and semi-natural sites (Wilson et al., 2012 and literature cited therein). Plant productivity~~,~~ or biomass, has been considered by some authors to be basic ecosystem characteristics (Laughlin, 2011; McLaren and Turkington, 2010). Abundance of plants has a preliminary influence on the quantity of exudates and plant remnants the soil receives (Bastida et al., 2008a; Bastida et al., 2008b). Other studies have used, among others, the soil carbon and nitrogen contents to assess the quality of ecosystem functioning (Mokany et al., 2006). Attempting to understand how the dominant species, with higher mean biomass, influence vegetation diversity and below ground parameters in the substrate is one of the possible approaches to understand development of a post-industrial ecosystem (Markowicz et al., 2015). Ecosystem functioning is related to the specificity of habitats of the newly developing ecosystem (Costanza et al., 1997; Kompała-Bąba et al. 2019). Differences in the amount of biomass recorded among the vegetation patches analysed (different dominant plant species) suggests the variety of ways in which particular vegetation patches influence the processes of development of post-industrial ecosystem functioning (Piekarska-Stachowiak et al., 2014; Stefanowicz et al., 2015).

In contrast to post-industrial areas, natural and semi-natural habitats are well recognized in terms of relationships between biomass production and biodiversity, as well as their role in shaping ecosystem functioning (Liang et al., 2016). However, most of the studies on plant species diversity were not related to the soil (Pereira et al., 2010; Tropek et al., 2017; Wilson et al., 2012). Our study revealed how the dominant plant species shape complex and highly variable relationships between the functional diversity of the vegetation associated

with the dominant species and soil substratum (abiotic and biotic), in terms of their habitat-shaping (above ground and below ground) parameters on human-created, post-industrial coal mine spoil heaps. These relationships reflect similar patterns known from natural and semi-natural ecosystems. Our study revealed that the highest species richness occurred in vegetation patches dominated by *Poa compressa*. However, this species does not achieve the highest biomass among the dominant species studied. In patches dominated by *Calamagrostis epigejos* values of vegetation cover, CWMs of specific leaf area and canopy height were significantly higher. This corresponds with the theory of biodiversity-productivity relationships, which indicates that the highest species diversity will be in the region with intermediate productivity (Mittelbach et al., 2001; Tilman, 1999; Wilson et al., 2012). Thus, differences in ecological requirements of the dominant species determine spatial heterogeneity and gamma diversity of post-industrial areas (Piekarska-Stachowiak et al., 2014).

The effects of dominant species on ecosystem functioning have been better described in reclaimed forests (e.g. Horodecki and Jagodziński, 2017; Rawlik et al., 2018b). The impacts of dominants are mostly manifested in the soil chemistry and understory species composition, due to the different elemental contents of tree biomass and the high biomass of trees, in contrast to the herbaceous species studied. For example, Rawlik et al. (2018b) found differences in soil P, K, Mg, Ca and Fe contents among stands of five dominant tree species. In our previous studies we also detected the effects of some dominant species on physicochemical soil parameters (Stefanowicz et al. 2015).

Contrary to our expectations, the species richness and functional diversity parameters were not lowest in patches dominated by the expansive grass *Calamagrostis epigejos*. Species richness was highest in patches dominated by *Poa compressa*. Surprisingly, functional divergence and functional richness were significantly higher in patches dominated by

Calamagrostis epigejos and were lowest in patches dominated by *Tussilago farfara*. High functional divergence in a vegetation patch indicates a high level of niche differentiation, and thus competition for different resources (low selection by environmental filtering) (Kraft et al., 2015). Thus, vegetation assemblages with high functional divergence may have increased ecosystem functioning as a result of higher effective resource utilization (de Bello et al., 2013; Podani et al., 2013). High functional richness and divergence are indicators of low environmental filtering (Laliberté and Legendre, 2010). However, in our previous studies we did not find any support for these two indices as indicators of harsher habitats (Czortek et al., 2018; Dyderski et al., 2017). In the studied system we may assume that higher functional divergence and functional richness in *Calamagrostis epigejos* may be an effect of the stronger dominance of this species. The other species occurring in patches dominated by *Calamagrostis epigejois* were usually a random admixture, representing various guilds, but which were never able to increase their contribution to the plant community. Thus, their different traits extended the community volume within the trait hyperspace.

In our study the amount of magnesium (Mg) was significantly higher under the vegetation patches dominated by *Daucus carota*, while the lowest amount of Mg was recorded under vegetation patches dominated by *Tussilago farfara*. Due to its unique chemistry, Mg is subject to various cycling processes within ecosystems. The important role of magnesium is connected with its high mobility (Cakmak and Yazici, 2010; Karley and White, 2009). In this respect the vegetation type, and its species composition, is very important in newly developing post-industrial ecosystems (Bose et al., 2011; Shaul, 2002). Magnesium plays an important role in increasing a plant's tolerance to various stresses, which influences its biomass (Gransee and Führs, 2013). The soil property found to be the most clearly influenced by different species was organic carbon (TOC). Contrary to our expectations it was highest in patches dominated by *Tussilago farfara*. In our study the

dominant species *Tussilago farfara* did not achieve the highest biomass, but this species had the highest leaf mass and leaf area. It also prefers soils with a high clay content, which are usually fertile and rich in organic matter (Namura-Ochalska, 1993). On coal-mine spoil heaps patches with *Tussilago farfara* are confined to gravelly, sandy or stony substrates (Kompała-Bąba et al. 2019).

The highest potassium (K) content was found in the substrate taken from vegetation patches dominated by *Tussilago farfara.* The K content was lowest in the vegetated plots dominated by the species with the lowest biomass, *Daucus carota.* It has been stated that the optimal potassium (K+): sodium (Na+) ratio is vital to activate enzymatic reactions in plants (Wakeel, 2013). Although most soils have adequate amounts of K+, in many soils the available K+ has become insufficient (Wakeel, 2013). The balance of elements on post-industrial sites depends on the mineral composition of stones and rocks which have been randomly gathered into coal mine spoil heaps. The habitat-shaping role of spontaneous vegetation in such cases is particularly important.

In many studies sodium (Na+) is reported as a toxic ion which affects plant growth by its detrimental influence on plant metabolism in inhibiting enzyme activities (Wakeel, 2013). It is reported that the available K+ can become insufficient in many sites (Mishra et al., 2015). The deficiency of K content is exacerbated partially as a consequence of K to Na antagonism. This is interesting, as in coal mine post-industrial sites the amount of potassium is significantly higher under the vegetation patches dominated by *Tussilago farfara* and *Poa compressa,* but no differences in the amount of Na+ and conductivity were recorded under any of the studied vegetation types. This is important considering that K+ uptake by plants is severely affected by the presence of Na+ in the nutrient medium (Mishra et al., 2015).

We also found the highest P content under the vegetation patches dominated by *Tussilago farfara*. The plant phosphorus concentrations and its SOM input depend on many

factors including soil parameters (coal mine spoil heap soil substrate) and plant growth form (Chen et al., 2018; Tang et al., 2018).

In terms of abiotic parameters, the presence of vegetation did not influence the conductivity and sodium content in the substrate on the surface of the coal mine spoil heaps. These results confirmed our previous findings where we did not find differences of electrical conductivity among vegetation plots with different dominant species, but electrical conductivity decreased with time as soluble salts were leached from the upper soil layers. Surprisingly, the presence of vegetation did not influence the total nitrogen content. Other studies conducted on coal mine spoil heaps and also other post-industrial sites have reported that generally nitrogen is below the detectable level. It has been stated that the presence of vegetation influences the value of surface pH on coal mine spoil heaps. In our previous studies substrate pH hardly differed among vegetation types (dominated by *Tussilago farfara, Calamagrostis epigejos* or *Chamaenerion palustre*), between plots with or without vegetation, or among spoil heaps of different ages. It ranged over 1.5 to 4 pH units (Stefanowicz et al. 2015). According to the ‘‘diversity hypothesis’’ the more diverse a given community is, then the higher resource utilization by species possessing different functional traits is, because of lower niche overlap (Tilman et al., 1997). Therefore, diverse communities influence ecosystem functioning because the entire pool of available resources is increased (Díaz and Cabido, 2001; Rao, 1982; Ricotta and Moretti, 2011). This is highly visible in natural and semi-natural plant communities (Grime and Mackey, 2002; Li et al., 2018; Loreau et al., 2002). The ‘mass ratio hypothesis’ explains that ecosystem functioning is mainly dominated by the traits of a dominant species (Grime et al., 1988). The more abundant species utilize a greater proportion of resources, thus the dominant species contribute disproportionately to ecosystem functioning (Cadotte et al., 2011). In contrast, the species with low abundances are relatively less important (Laughlin, 2011).

Our results have revealed the superior role of dominant plant species in the recovery of post-industrial sites. We found that the studied vegetation types significantly influenced the biological activity of coal mine spoil heaps. Dehydrogenase and alkaline phosphatase activity was highest under the patches dominated by *Poa compressa,* whereas acid phosphatase activity was highest under the patches dominated by *Calamagrostis epigejos*. These effects may be used to accelerate reclamation processes and may help to predict the course of reclamation on areas left to spontaneous succession. This may be related to the fact that the grasses have a well-developed root system (De Baets et al., 2006), which is associated with the secretion of large amounts of root exudates (Bąba et al., 2016; Mommer et al., 2010; Ravenek et al., 2014). A large number of fine roots and their exudates stimulate the development of arbuscular mycorrhizal fungi (AMF) and other microorganisms, largely responsible for the activity of soil dehydrogenase (Wolińska and Stępniewska, 2012). In addition, the roots of plants and AMF have been proven to be the main source of acid phosphatase in the soil, while the bacteria mainly produce alkaline phosphatase (Sakurai et al., 2008).

Our study has provided comprehensive evidence that dominant species in the spontaneous vegetation developing on post-industrial sites alter its species and functional composition, as well as the chemical and biological properties of the soil substrate. Despite our assumptions (Hypothesis 1), the species with the highest mean biomass (*Calamagrostis epigejos*) did not cause lower species or functional divergence in its vegetation patches than e.g. *Tussilago farfara*, that had the second highest mean biomass. We also found that as a dominant plant, *Tussilago farfara* seemed to have the highest impact on the habitats formed on post-industrial coal mine spoil heaps, compared to the other species studied. This contradicts hypothesis 2, which assumed the highest impact by *Calamagrostis epigejos*. Four of the soil substratum parameters (TOC, P, K, N) were recorded at their highest levels under

vegetation patches dominated by *Tussilago farfara*. This suggests that the habitat-shaping role of *Tussilago farfara* is considerable, regardless of the fact that the species number and functional divergence was lowest in *Tussilago farfara* dominated patches and that the biomass of these patches was intermediate.

Conclusions

The relationship between the vegetation types studied did not always follow the known rules for natural or semi-natural vegetation. The results indicated that developing novel ecosystems are not well understood and require further study; otherwise, reclamation and restoration processes will be insufficient or will fail. Dominant species utilize existing resources on post-industrial sites in different ways and they also influence both aboveground and belowground species and functional diversity in different ways. Obtaining knowledge about relationships existing between plants (aboveground vegetation) and soil organisms seems extremely important to undertake suitable reclamation or restoration measures, to restore a variety of ecosystem functions, and to create diverse vegetation based mainly on native species.

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Figure

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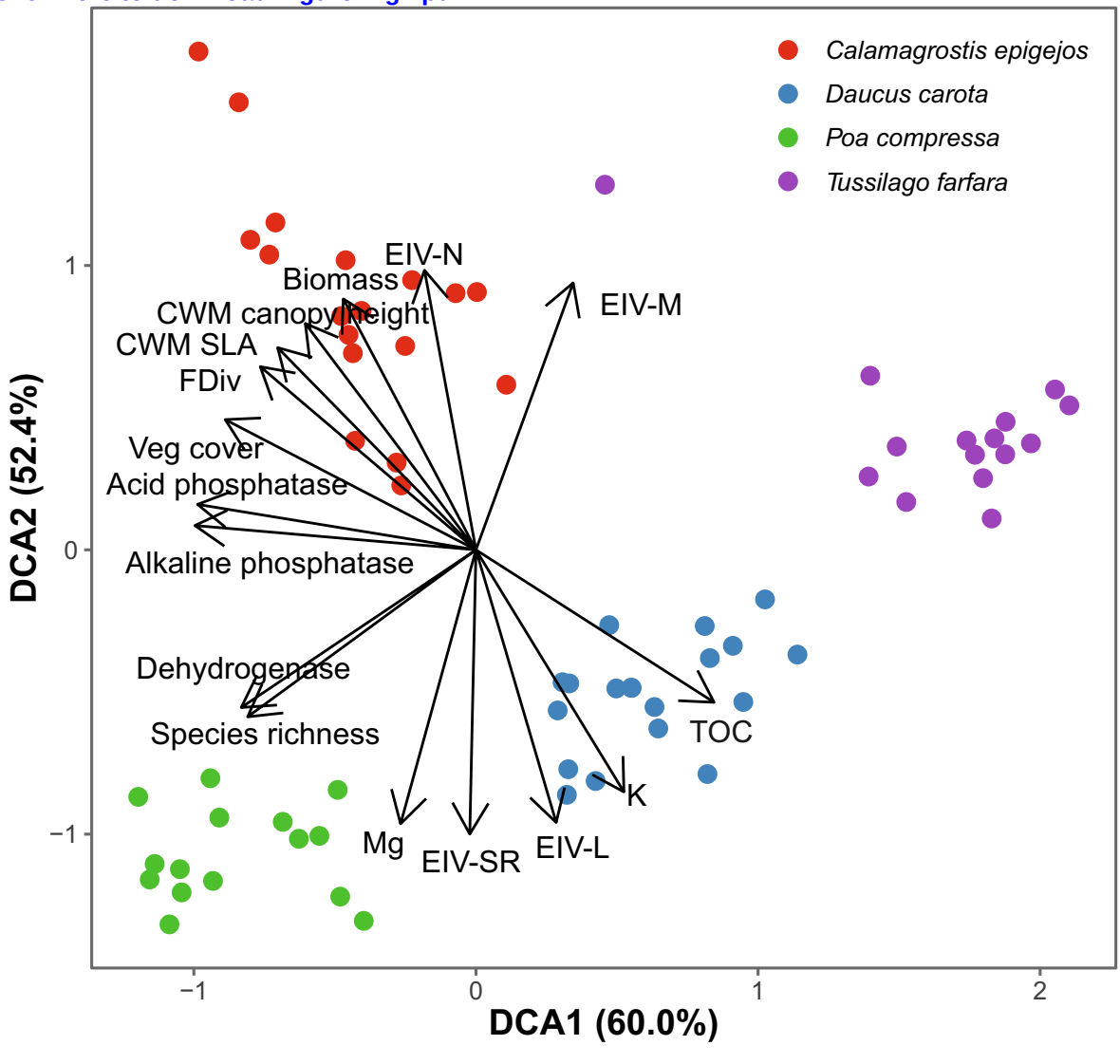

Table1

Table 1. Overview of species ecology, according to the BiolFlor database (Klotz et al. 2002), ecological indicator values (EIVs; Ellenberg and Leuschner 2010) and LEDA functional traits database (Kleyer et al., 2008).

Parameter	*Poa compressa*	*Calamagrostis epigejos*	*Daucus carota*	*Tussilago farfara*
Family	Poaceae	Poaceae	Apiaceae	Asteraceae
Life strategy	csr	c	cr	csr
Life form	hemicryptophyte	hemicryptophyte/geophyte	hemicryptophyte	geophyte
Pollen vector	wind	wind	self-compatible/ insects	self-compatible/ insects
EIV-Light	9	7	8	8
EIV-Temperature	NA	5	6	NA
EIV-Continentality	4	7	5	3
EIV-Moisture	3	NA	4	6
EIV-Soil reaction	9	NA	NA	8
EIV-Soil nutrients	3	6	4	NA
Canopy height	0.375	1.000	0.393	0.185
Leaf dry matter content [mg g^{-1}]	282.333	400.033	232.045	139.000
Leaf mass [mg]	7.363	258.194	12.840	2873.927
Leaf size [mm^2]	170.000	4994.500	NA	48997.500
Specific leaf area [mm^{-2} g^{-1}]	19.420	15.680	19.564	19.625
Seed mass [mg]	0.205	0.080	1.163	0.225
Seed number per shoot	19450.300	173453.086	32745.222	5842.167

Table

Table 2. Mean and SE of soil parameters for plots dominated by the species studied and plots without vegetation. Groups marked by the same letter in a row do not differ statistically significantly at p=0.05, according to Tukey's *posteriori* test. The highest value is indicated in bold.

	No. vegetation plots			*Calamagrostis epigejos*			*Daucus carota*			*Tussilago farfara*			*Poa compressa*			ANOVA	
Parameter	mean	SE		mean	SE		mean	SE		mean	SE		mean	SE		F	p(>F)
pH in KCl	4.275	0.334	b	5.789	0.278	a	6.116	0.156	a	5.378	0.364	a	**6.230**	**0.146**	**a**	8.652	<0.001
pH in H_2O	4.684	0.315	b	6.347	0.234	a	6.633	0.127	a	5.836	0.357	a	**6.829**	**0.141**	**a**	12.048	<0.001
Conductivity	0.309	0.085	a	0.232	0.029	a	0.361	0.044	a	0.268	0.039	a	**0.481**	**0.125**	**a**	1.871	0.124
TOC	13.370	1.335	ab	9.850	1.620	b	12.484	1.030	ab	**18.687**	**2.227**	**a**	13.640	1.844	ab	3.860	0.006
K	141.550	16.921	c	171.689	13.808	bc	229.832	18.070	ab	**266.160**	**37.754**	**a**	233.680	18.827	ab	5.223	0.001
Mg	246.906	28.718	bc	270.444	21.122	abc	**327.447**	**9.638**	**a**	190.933	20.523	c	303.967	17.977	ab	6.803	<0.001
N	0.279	0.023	a	0.255	0.033	a	0.275	0.018	a	**0.304**	**0.041**	**a**	0.302	0.041	a	0.409	0.802
Na	41.700	3.880	a	57.244	10.363	a	**94.737**	**24.628**	**a**	48.213	11.007	a	91.387	33.682	a	1.566	0.192
P	4.240	0.902	b	10.644	1.904	ab	10.353	1.548	ab	**12.432**	**2.181**	**a**	12.319	2.184	a	3.355	0.014
Dehydrogenase	9.954	2.233	b	101.404	52.502	ab	56.847	27.223	ab	24.688	4.510	ab	199.160	78.906	a	2.801	0.032
Acid phosphatase	431.614	143.434	bc	**1164.574**	**226.403**	**a**	329.029	53.590	c	260.172	34.649	c	1070.835	226.476	ab	7.441	<0.001
Alkaline phosphatase	167.930	32.978	c	1606.191	322.116	ab	952.820	220.673	bc	545.860	130.057	c	**1966.078**	**287.971**	**a**	9.349	<0.001
Urease	0.137	0.032	a	0.221	0.041	a	0.121	0.022	a	0.145	0.020	a	**0.167**	**0.022**	**a**	1.913	0.117

Table

Table 3. Mean and SE of vegetation parameters for plots dominated by the species studied and plots without vegetation. Groups marked by the same letter in a row do not differ statistically significantly at p=0.05, according to Tukey's *posteriori* test. The highest value is indicated in bold.

	Calamagrostis epigejos			*Daucus carota*			*Tussilago farfara*			*Poa compressa*			ANOVA	
Parameter	mean	SE		mean	SE		mean	SE		mean	SE		F	p(>F)
Biomass	**66.367**	**9.581**	**a**	14.903	1.430	b	38.437	6.172	b	29.102	5.260	b	12.702	<0.001
Vegetation cover	**71.667**	**4.220**	**a**	44.211	3.613	b	40.667	2.482	b	62.667	5.115	a	14.052	<0.001
Species richness	12.889	1.075	a	12.842	0.777	a	8.267	0.802	b	**14.067**	**0.959**	a	7.096	<0.001
CWM canopy height	**0.884**	**0.032**	**a**	0.471	0.017	b	0.342	0.036	c	0.501	0.014	b	80.369	<0.001
CWM seed mass	**3.196**	**2.150**	**a**	1.024	0.059	a	0.409	0.037	a	0.527	0.024	a	1.287	0.287
CWM SLA	**23.445**	**0.533**	**a**	21.165	0.140	b	20.479	0.172	b	21.488	0.288	b	14.905	<0.001
FDis	**0.201**	**0.011**	**a**	0.191	0.005	a	0.185	0.016	a	0.190	0.005	a	0.501	0.683
FDiv	**0.837**	**0.041**	**a**	0.734	0.024	ab	0.680	0.056	b	0.765	0.020	ab	3.123	0.032
FEve	0.735	0.017	a	0.712	0.020	a	0.716	0.044	a	**0.740**	**0.013**	**a**	0.310	0.818
FRic	**0.876**	**0.118**	**a**	0.790	0.088	ab	0.490	0.079	b	0.708	0.043	ab	3.241	0.028
EIV-L	7.286	0.034	c	7.891	0.042	b	7.876	0.055	b	**8.194**	**0.057**	**a**	50.523	<0.001
EIV-M	5.236	0.213	b	4.365	0.062	c	**5.840**	**0.065**	**a**	3.731	0.058	d	67.262	<0.001
EIV-N	**5.561**	**0.135**	**a**	4.305	0.072	bc	4.860	0.313	b	3.971	0.070	c	17.933	<0.001
EIV-SR	6.675	0.168	b	6.914	0.151	b	7.722	0.060	a	**8.193**	**0.091**	**a**	27.195	<0.001

Supplementary Material

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***Conflict of Interest**

We did not have any conflict of interests as regards this manuscript.